Age determination of land mammals from annuli

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Laws (1962) in this Journal has reviewed thoroughly the use of growth layers in the teeth as well as other methods for determining the age of seals. To quote him, "the best methods ... are based on variations in the rate of deposition of tooth material which are visible as external annuli on the root and/or as distinct growth layers seen in sections of the dentine and cementum". These methods have been applied also to Odontocete whales, while in Mysticeti a layered structure, the earplug of the external auditory meatus, was discovered as an indicator of age.

Laws (1953), in his preliminary study of the methods, made a rapid external examination of the teeth of a number of vertebrates (other than sea mammals), living and extinct, and found growth ridges on the root of the teeth in the following: canine of Carnivora (*Hyaena, Felis, Ursus*), incisor of Proboscidea (*Mastodon, Elephas*), molar of *Rhinoceros,* canine of *Sus,* canine and incisor of *Hippopotamus,* molar of *Bison,* and teeth of fossil reptiles (*Ichthyosaurus, Pliosaurus, Mosasaurus, Dacosaurus*).

Workers on land mammals have been slow to explore the methods, and no thorough study has yet been made of a range of mammals and reptiles, tropical and temperate by origin, living and extinct, which would make possible a wide review of the subject of periodic layering in skeletal tissues and its possible causes. The purpose of this preliminary review is rather to draw attention to the methods.

More than half the studies so far published have dealt with Cervidae of the northern hemisphere. These are listed in the table. Some general conclusions may be stated.

Studies of age determination in Ungulates from cemental layers in the teeth

Species		Tooth	Authors
Alces americanus	Moose	I_1	Sergeant and Pimlott, 1959
Cervus elaphus	Red Deer	M_1	Mitchell, 1963
Odocoileus hemionus	Black-tailed deer	I^1	Low and Cowan, 1963
Odocoileus virginianus	White-tailed deer	M_1	Gilbert, 1966
Odocoileus virginianus	White-tailed deer	M_1	Ranson, 1966
Rangifer tarandus	Caribou	I_1	McEwan, 1963

1. Clear zonation is found in the cementum, but not in the dentine, of both incisors and molars. Workers have usually selected the first permanent tooth to erupt e. g. I^1 in *Odocoileus hemionus,* M_1 in *Cervus elaphus* C. The method of preparation has been to section longitudinally the root of the tooth, and either to examine the surface of the cut cementum under reflected light, or to cut thin sections and usually to decalcify and stain them. While the former method is rapid, the latter gives more detail. Since cementum deposits unevenly, it is important to examine the thickest part with maximum number of layers. With this proviso the number of layers is found to be consistent in paired teeth, and is greater in teeth that erupt earlier.
2. Each layer consists of a zone of wide, opaque, well-calcified tissue which takes up

little haematoxylin, and a narrow, translucent zone in which the more frequent biolamellae take up the stain.

3. From studies made through the year, it has been established that the opaque zone is laid down in the summer months and the fibrous zone in the winter months. Sometimes the fibrous zone is double, a narrow zone of well-calcified growth being enclosed by a growth-check in autumn and one in late winter (Low and Cowan, 1964).
4. From known-age animals, the number of layers is equal to the age in years, after addition of the period of early life before calcification of the particular tooth begins.

Bergerud and Russell (1966) report that in caribou *(Rangifer)* the small second or third incisor may be removed from the living animal for age determination, without injury resulting.

Among the Carnivora, four studies have been published on Ursidae and one on Canidae. In the black bear *Ursus americanus* Rausch (1961) noted ridges on the root of the canine, which he attributed to seasonal growth of the dentine, and correlated with age. However, Marks and Erickson (1966) with known-age material did not find this method reliable. They found clear layering in the cementum of canines of black bears, and found this to be the most reliable of several aging methods which they studied. Cemental layering had previously been found in M_3 of grizzly bear *Ursus arctos* subsp. by Mundy and Fuller (1964), and Stoneberg and Jonkel (1966) have confirmed the method in this species, having known-age material and using canine teeth. In these bears the zonation is similar to that found in Cervidae, a wide zone of non-staining cementum being laid down in summer, a narrow fibrous zone of deeply-staining cementum in winter. The layering ist clearer than in most Cervidae, which fact has been correlated with the contrast between the periods of the bears' activity and hibernation. However, Stoneberg and Jonkel noted that deposition of winter-type cementum begins before hibernation begins. I have observed clear layering in the cementum of canine teeth of polar bear *Ursus maritimus*.

In the arctic fox *(Alopex lagopus)*, cemental layering is found in molars and canines, and known-age animals from fox farms have shown that the layers are annual (Kleinenberg and Klevezal', 1966).

Among Rodentia, Kleinenberg and Klevezal' (1966) show clear layering in molars of beaver *(Castor fiber)* with the same pattern of layering as noted in other northern animals.

Even in such a short-lived animal as a shrew, *Sorex araneus*, these authors find that the root of the molar shows a check in growth associated with wintering.

As well as in teeth, layering is found in the outer periostal zone of bones. Such layering was first described in the mandible of seals (Chapskii, 1952) and of toothed whales (Laws, 1960, Nishiwaki, Ohsumi and Kasuya, 1961), and in the auditory bulla of seals (Laws, 1953b). The number of bone layers usually corresponds with the number of layers in tooth dentine, although in *Delphinus delphis* Kleinenberg and Klevezal' (1963) found twice as many dentinal layers as bone layers. In beaver, Kleinenberg and Klevezal' (1966) find bone layers and cemental layers in the teeth to be equal in number. At higher ages (about 10–15 layers in seals and sperm whales, *Physeter*), the inner bone layers are absorbed as fast as new ones are formed and the indicated age attains a plateau.

A wide survey of layering in the periostal zone of limb bones of mammals has been made by Klevanova and Klevezal' (1966) who state that "in most rodents, Lagomorpha, carnivores, some marsupials, Edentata, Chiroptera and primates distinct layers separated by cement lines are recorded in the periostal zone of tubular bones. The numbers of layers found in the animals belonging to different species did not

exceed the maximal possible age of the species expressed in years . . ." "The formation of layers in the periostal zone can be regarded as a manifestation of seasonal changes in the bone growth that seem to be intrinsic to the majority of mammals."

As has long been known, alternating slow and rapid growth occurs in the horns of northern sheep *(Ovis canadensis, O. dalli)* and goat-antelopes *(Oreamnos americanus)* resulting in the formation of annual ridges on the surface (Mosby, 1963). These may be compared with growth ridges in the claws of seals (see Laws, 1962). According to Mosby, in Bighorn sheep Cowan (1940) suggested that the checks represented cessation of growth during the breeding season, although other authors suggested a direct effect of nutrition.

Significance of Layering

Since many species of land mammals may be reared in captivity the opportunities for determining the physiological basis of layering are much greater than in sea mammals.

Wood, Cowan and Nordan (1962) studied the detailed annual cycle of body growth in individual deer *Odocoileus hemionus*. Growth of captive animals reared at a constant high ration showed a seasonal pattern. Body growth ceased at 5—6 months, as a result of voluntary reduction of food intake, the change being associated with onset of rutting behaviour and thus indicating attainment of puberty. However, growth continued and maturity was delayed if the animals were kept at a low ration. After the first year of life, weight changes were more regular, a phase of rapid growth in spring invariably slowing in summer and being followed by weight loss in winter. This pattern was found in both sexes, though the seasonal weight fluctuation was less in females, which underwent less marked physiological changes at the rut. An appreciable part of the annual spring and summer weight-gain represented an accumulation of adipose tissue, while the winter weight loss was largely accounted for by the disappearance of these fat deposits. The fundamental mechanisms underlying the profound alterations in the growth curve, and hence probably in metabolism, were considered to be associated with reproduction. McEwan and Wood (1966) showed a very similar growth cycle in captive caribou *Rangifer tarandus;* again the seasonal cycle of food intake and growth persisted even in well-fed animals.

In Cervidae, therefore, the period of rapid body growth is contemporary with the deposition of wide zones of well-calcified cementum. Thus, the type of cemental growth is dependent upon nutritional state. Since body growth of captive Cervidae fed a high ration declines at the rutting season, sex hormones reduce food intake and presumably cemental growth also. This conclusion is supported by the observation of Low and Cowan that in the wild two growth checks may occur, the first associated with the rut and the second with late winter conditions. As several authors have pointed out, study of species from different environments (e. g. deer from grassland with summer drought) may help to disentangle the direct effects of environment from intrinsic rhythms. It is clear also that further experimental, including endocrinological, work will be profitable.

Summary

Growth layers have been found in the cementum, but not in the dentine, of a number of species of northern Cervidae (deer), Carnivora (bears, fox) and one rodent (beaver), hitherto examined. They have allowed age to be determined to within one year. Layers in the periostal zone of bones are widespread in mammals and in at least one instance (beaver) correspond in number with cemental growth layers. In at least two species of deer, cemental deposition is closely linked to the seasonal sequence of body growth which persists at a constant high ration of food and is therefore intrinsic, controlled by sex and perhaps other hormones.

Zusammenfassung

Wachstums-Ringe wurden gefunden — soweit danach gesucht wurde — im Zement, jedoch nicht im Dentin einer Anzahl Arten nordischer Cerviden (Hirsche), Carnivoren (Bären, Füchse) und Rodentiern (Biber). Diese Ringe im Zement erlaubten, das Alter bis zu einem Jahr genau zu bestimmen. Wachstumsringe in der periostalen Zone von Knochen sind bei Säugetieren weit verbreitet, und in wenigstens einem Fall (Biber) stimmen sie mit den Ringbildungen im Zement überein. Bei wenigstens 2 Hirsch-Arten hängt die Ablagerung von Ringen im Zement eng zusammen mit dem jahreszeitlichen Ablauf des Körperzustandes, der auch durch innere Faktoren mit beeinflußt und durch Geschlechts- und wahrscheinlich noch weitere Hormone gesteuert wird.

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